Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins

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Abstract: Socially learned behaviours leading to genetic population structure have rarely been described outside humans. Here, we provide evidence of fine-scale genetic structure that has probably arisen based on socially transmitted behaviours in bottlenose dolphins (Tursiops sp.) in western Shark Bay, Western Australia. We argue that vertical social transmission in different habitats has led to significant geographical genetic structure of mitochondrial DNA (mtDNA) haplotypes. Dolphins with mtDNA haplotypes E or F are found predominantly in deep (more than 10 m) channel habitat, while dolphins with a third haplotype (H) are found predominantly in shallow habitat (less than 10 m), indicating a strong haplotype-habitat correlation. Some dolphins in the deep habitat engage in a foraging strategy using tools. These 'sponging' dolphins are members of one matriline, carrying haplotype E. This pattern is consistent with what had been demonstrated previously at another research site in Shark Bay, where vertical social transmission of sponging had been shown using multiple lines of evidence. Using an individual-based model, we found support that in western Shark Bay, socially transmitted specializations may have led to the observed genetic structure. The reported genetic structure appears to present an example of cultural hitchhiking of mtDNA haplotypes on socially transmitted foraging strategies, suggesting that, as in humans, genetic structure can be shaped through cultural transmission.

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Cultural transmission of tool use combined with habitat specialisations leads to fine-scale genetic structure in bottlenose dolphins

Kopps, Anna M.[a,b] (anna.kopps@gmx.com), Ackermann, Corinne Y.[b], Sherwin, William B.[a,c], Allen, Simon J.[c], Bejder, Lars[c] & Krützen, Michael[b,a]

[a]Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

[b]Evolutionary Genetics Group, Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

[c]Murdoch University Cetacean Research Unit, Centre for Fish, Fisheries and Aquatic Ecosystems Research, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, WA 6150, Australia

Abstract

Socially learned behaviours leading to genetic population structure have rarely been described outside humans. Here, we provide evidence of fine-scale genetic structure that has likely arisen based on socially transmitted behaviours in bottlenose dolphins (*Tursiops* sp.) in western Shark Bay, Western Australia. We argue that vertical social transmission in different habitats has led to significant geographic genetic structure of mitochondrial DNA (mtDNA) haplotypes. Dolphins with mtDNA haplotypes E or F are found predominantly in deep (> 10m) channel habitat, while dolphins with a third haplotype (H) are found predominantly in shallow habitat (< 10m), indicating a strong haplotype-habitat correlation. Some dolphins in the deep habitat engage in a foraging strategy using tools. These "sponging" dolphins are members of one matriline, carrying haplotype E. This pattern is consistent with what had been demonstrated previously at another research site in Shark Bay, where social vertical transmission of sponging had been shown using multiple lines of evidence. Using an individual-based model, we found support that in western Shark Bay, socially transmitted specialisations may have led to the observed genetic structure. The reported genetic structure appears to present an example of cultural hitchhiking of mtDNA haplotypes on socially transmitted foraging strategies, suggesting that, as in humans, genetic structure can be shaped through cultural transmission.

Key index words: bottlenose dolphin, cultural hitchhiking, genetic structure, *Tursiops* sp., social learning

Introduction

Darwinian selection acts on phenotypes, which are manifested through both genetically and non-genetically inherited traits. Both inheritance mechanisms may be adaptive and, thus, of evolutionary consequence [1]. Vertical social transmission (i.e., learning from a biological parent) closely follows genetic inheritance patterns. For example, the diets and/or foraging strategies of offspring have been shown to resemble that of their mother in a wide range of mammalian taxa (e.g. orangutans *Pongo pygmaeus wurmbii*, sea otters *Enhydra lutris nereis* and bottlenose dolphins *Tursiops* sp.) [2-4]. All three species share prolonged maternal dependence and there is overlap between nursing and offspring-foraging during development, providing opportunities for social learning [2, 3, 5].

Social transmission can affect the evolutionary outcomes of genetic transmission and vice versa. Social transmission may change selection pressure on genes [gene-culture coevolutionary theory, 6], as for example documented for the spread of lactose tolerance in adult humans [7] and proposed for hundreds of human genes [8]. Further, individual learning capacity or the exposure to a socially learned trait can correlate with specific genetic marker systems [6]. For instance, in vertical social transmission, patterns of transmission of the socially learned trait and uniparentally inherited genetic units, such as mitochondrial DNA (mtDNA), and the Y chromosome, may be closely correlated. If the socially learned trait increases its bearer's fitness, population frequencies of these correlated genetic units will increase, even if there is no other active selection on genetic units. This phenomenon is called "cultural hitchhiking" [9] and was posed as a possible explanation for the low genetic diversity in human mtDNA and Y chromosome sequences [10] and the low mtDNA diversity in matrilineal whales [9]. However, stochastic modelling has shown that a

58 reduction of genetic diversity is not a necessary consequence of parallel transmission of
59 genes and socially-learned phenotypes [10, 11].

60 Cultural hitchhiking might occur with little or no fitness differences if there is fine-scale
61 geographic population structure that relates to the cultural trait, as we discuss below. There
62 are two general types of geographic population structure: continuous clines or sharp
63 boundaries [12]. Genetic and geographic distances often correlate in natural populations
64 [i.e. isolation-by-distance, e.g., 13]. On the other hand, geographic features resulting in
65 habitat fragmentation or behavioural patterns limiting movement and genetic exchange,
66 may lead to discontinuous genetic structuring of populations. There is ample evidence for
67 structuring by geographical boundaries [14]. However, there is limited evidence for
68 geographic structuring of genetic variation due to behaviour and even less evidence due to
69 cultural behaviour. Possible mechanisms include assortative mating and microhabitat
70 specialisation. For example, two species of cichlid fish (*Amphilophus xiloaensis* and *A.*
71 *sagittae*) preferentially mate with a partner of the same colour morph, which has led to
72 genetic differentiation between morphs [15]. Moreover, in killer whales (*Orcinus orca*),
73 socially transmitted foraging specialisations within an ecosystem were proposed to have led
74 to sympatric ecotypes in the absence of physical barriers [16, 17].

75 To date, studies describing the influence of social transmission or culture on genetic
76 structure or selection have focused on genetic variation between populations [8]. Here, we
77 provide an example of how social transmission may drive genetic structure within a single
78 dolphin population.

79 Thirteen foraging strategies have been described for bottlenose dolphins in the eastern gulf
80 of Shark Bay (ESB), Western Australia [3]. Individual females have been observed to engage

in one to seven of these strategies [3], some of which are only observed in specific habitats. The most prominent foraging strategies observed only in shallow water include beach hunting, bottom grubbing and kerplunking [18, 19]. Foraging strategies observed in deep water include 'sponging' [20-23]. The question of whether sponging is a socially transmitted behaviour has been studied extensively in Shark Bay in the past [3, 20, 21, 24-28]. These studies used different approaches (i.e. genetics, individual follows, survey data, network-based approaches, individual based modelling or combinations thereof) to infer social transmission of tool use in this population.

Sponging dolphins ('spongers' hereafter) carry conical marine sponges on their rostrums, most likely to protect them while foraging for prey hiding in the substrate [21, 27]. The behaviour is almost exclusively vertically transmitted from mothers to their offspring through social learning [3, 20, 24]. With one exception, spongers in ESB share a maternally inherited mtDNA haplotype [24]. Spongers in ESB are also biparentally more closely related than expected by chance [24]. Haplotype sharing between sponging individuals is expected in cases of strong vertical social transmission [24].even though a genetic basis for sponging has been ruled out [24, 25, 28], Sponging has also been documented in the western gulf of Shark Bay (WSB) [23, 25, 29]. The ESB and WSB study sites are approximately 120 km apart by sea divided by a prominent peninsula and there is no direct evidence of dispersal between the sites [30]. In both gulfs, sponging is almost exclusively limited to deep channels where sponges occur [22, 23]. However, not all individuals inhabiting deep channels use sponges to forage. Therefore, a purely ecological explanation for sponging would not account for the heterogeneity of foraging strategies observed in these deep channels [22, 24].

This study focuses on the fine-scale population genetic structure of bottlenose dolphins in WSB. We investigated the relationship between maternal relatedness, habitat and behaviour. Our study significantly extends previous studies in that it explores the possibility of social transmission shaping genetic structure in an animal population. This is a very important advance because, to our knowledge, our study provides the first example of the potential impact of social learning on within-population structure in non-human animals (as opposed to its influence on between-population structure [15-17]). Briefly, we observed striking spatial homogeneity in mtDNA, in contrast to other parts of the bay where haplotype distribution was much more heterogeneous [30]. We aimed to test the hypothesis that vertical social transmission of a habitat-dependent trait can lead to fine-scale genetic structure. To do this we modelled the possible process using an individual-based model based on empirical data. We used this model to investigate whether the observed homogenous mtDNA haplotype structure could be a result of a random process, or alternatively, would require that transmission patterns of a socially learned trait and uniparentally inherited genetic units correlate, as is already known in this case [3, 20, 21, 24-28]. Briefly, the model showed, that the observed geographic structuring of mtDNA haplotypes is only possible if genetic and social transmission are correlated.

Material and methods

(a) Study site and data collection

Shark Bay is located on the west coast of Australia, 850 km north of Perth. It consists of an eastern and western gulf, divided by Peron Peninsula. Our main study area is off the township of Useless Loop in the western gulf and consists of approximately 260 km^2, about five times the size of the average home range of an adult ESB bottlenose dolphin [31]. We will refer to our main study area as WSB. WSB is characterized by channels (> 10 m deep) dividing shallow water areas that are closer to land (figure 1) [23].

We carried out systematic photo-identification and behavioural surveys on bottlenose dolphins from a 5.4 m boat with an outboard motor. Dolphin group composition [10 m chain rule, 32], water depth, GPS and predominant dolphin activity (forage, rest, travel, social or unknown) were recorded. For our analyses we did not discriminate between these activities. Dolphins were individually identified by natural markings and the shape of their dorsal fin [33]. Biopsy sampling [34] was conducted under a License to use and/or supply Animals for Scientific Purposes from the Western Australian Department of Environment and Conservation, and ethics approval was obtained from the University of New South Wales (08/33B) and the University of Zurich.

A sponger was defined as a dolphin which was seen sponging at least twice [20]. We were able to use water depth as a proxy for habitat because Tyne *et al.* [23] reported that in WSB, sponges only occur in water deeper than 10 m, while seagrass occurs in shallow water (< 10 m).

(b) Analyses

144 The genetic sampling and laboratory methods are detailed in the supplement. We ran a
145 nested ANOVA in PASW Statistics 18 to test for significance of association between water
146 depth distribution of dolphins with different mtDNA haplotypes. Because multiple sightings
147 of the same individuals were included, individual dolphin identification (ID) was used as a
148 random factor. To exclude the possibility that the observed mtDNA haplotype distribution
149 might simply be an artefact of significant autosomal population structure, we tested
150 whether the observed segregation of mtDNA haplotypes and depth is reflected in
151 biparentally inherited microsatellite markers. Such autosomal structure would have to be
152 very strong, causing a severe restriction of gene flow, if it was to secondarily produce the
153 very clear mitochondrial geographic structuring. To investigate this, we ran a STRUCTURE
154 analysis (burn-in length of 10^5 and 10^6 Markov chain Monte Carlo steps) using mtDNA
155 haplotype as Locprior. [35-37]. The use of a Locprior model significantly increases the
156 chance to detect population structure even in weakly structured populations [37]

157 We analysed whether spongers shared an mtDNA haplotype more often than would be
158 expected by chance and whether they were biparentally more related than would be
159 expected by chance. Individuals (spongers and non-spongers) were included in these
160 analyses when they were sampled in an area specified by a 95% kernel utilization
161 distribution of locations where sponging had been observed by any animal [24] (figure S1).
162 The kernel was calculated in ArcMap 9.2 (ESRI) using the extension Home Range Tools [38].
163 Pairwise comparisons between the observed mtDNA haplotype distribution within spongers
164 were compared to pairwise comparisons of 10,000 times the number of sampled spongers
165 randomly drawn. The haplotype frequencies used as a basis for randomisation reflected the
166 frequencies calculated for the WSB dolphins. The randomizations were carried out in a
167 “macro” written in Microsoft Excel.

168 To test whether spongers are biparentally more related than expected by chance, we
169 calculated the average pairwise relatedness among spongers and compared it to the average
170 pairwise relatedness of the population. We calculated the Queller and Goodnight [39]
171 estimator of pairwise relatedness (R) in SPAGEDi [40]. In order to assess statistical
172 significance, we programmed a randomization test in MATLAB R2010a. Biparental genotypes
173 of all sampled individuals of the population were randomized and the average pairwise
174 relatedness among 22 or 15 (for WSB and ESB respectively, representing the number of
175 biopsy sampled spongers) randomly drawn genotypes were calculated. In the
176 randomization, the observed sex ratio of spongers was retained.

177 *(c)Individual-based model*

178 We used simulations to test the hypothesis that vertical social transmission of a habitat-
179 dependent trait can lead to fine-scale genetic structure using an individual-based model
180 based on empirical data. The model is described in detail in the supplement. We included
181 simulations of a null model with no fitness benefits for specialist, as well as one with fitness
182 benefits. Most simulations were run with 5% fitness benefits for specialists even though
183 empirical data suggest that fitness advantages of spongers may be larger than that, albeit
184 being non-significant [20].

185

186

187 **Results**

188 *(a) mtDNA haplotypes and habitat*

189 We found a strong and significant association between dolphin mtDNA haplotypes and
190 water depth in WSB. Dolphins with mtDNA haplotypes E or F were predominantly found in
191 deep water (> 10 m deep) and dolphins with haplotype H in shallow water (< 10 m, figures 1
192 and 2). The geographic segregation of mtDNA haplotypes in WSB was not reflected in
193 biparentally inherited genetic markers: STRUCTURE plots showed no indication of genetic
194 structure (figure S2). The depth distribution for both adult males and females with one of
195 the three common haplotypes E, F, and H differed significantly (tables 1 and 2), as revealed
196 by a nested ANOVA and a subsequent Tukey's HSD *post hoc* test, based on 90 dolphins (59
197 females and 31 males) and 756 sightings (mean number of sightings ± SE/individual: 8.4 ±
198 0.68, range = 1-33). Three other haplotypes (B, D, I) were rare (frequency < 0.03).

199 *(b) Genetic relatedness of spongers*

200 Forty spongers have been identified in WSB which represents about a quarter (25.9%) of
201 dolphins identified in deep water [29]. All 22 biopsied spongers in WSB share the same
202 mtDNA haplotype E, which is significantly different ($P < 0.001$) from what would be expected
203 by chance, based on the observed mtDNA haplotype frequencies in the population. The
204 sponger haplotype E in WSB is different from the haplotype found among ESB spongers
205 [haplotype H, 24]. All 22 sampled spongers were biparentally more closely related than the
206 population average ($R_{spongers} = 0.0259$, $R_{population} = -0.0104$, $N_{population} = 108$), although this
207 difference was not statistically significant ($P = 0.092$). We also re-ran the pairwise
208 relatedness analyses for ESB [24], including additionally genotyped microsatellite loci and
209 individuals. Our result confirms the previous publication [24]: spongers in ESB were found to

be biparentally more closely related than the population average and than expected by chance ($R_{spongers}$ = 0.0712, $R_{population}$ = -0.0044, $N_{spongers}$ = 15, $N_{population}$= 238, *P* = 0.006).

(c) *Individual-based model*

Simulations showed that fine-scale genetic structure based on mtDNA haplotypes can be driven by vertically, socially transmitted, habitat-dependent traits (figures 3, S3). The geographic segregation of haplotypes occurred even if the learning fidelity was not 100% (figure S3), but in the absence of vertically, socially transmitted specialisations, no geographic segregation of mtDNA haplotypes was observed (figure 3, fourth column).

Discussion

Through a combination of empirical data and individual-based modelling, we were able to infer that the vertical cultural transmission of a foraging behaviour involving tools has led to the clear separation of mtDNA haplotypes within our study area. The observed geographic distribution of dolphins with different mtDNA haplotypes might represent a case of cultural hitchhiking. To our knowledge, this is one of the first studies to provide evidence for fine-scale geographic genetic structure driven by socially transmitted behaviour within a single wild animal population.

In what circumstances would we predict correlations between habitats and mtDNA haplotypes? We propose that four prerequisites must be met. First, a population must exhibit vertically socially transmitted, habitat-dependent skills, such as foraging or predator avoidance strategies. Second, philopatry must keep haplotypes localised, although if one sex disperses, the pattern could still be found in the philopatric sex. Third, habitat differentiation needs to be on a scale that is larger than an individual's home range. Fourth, in order for habitat specialisations to drive genetic differentiation over small distances, these specialisations must be stable over an individual's life time [41] and also present in following generations. The clear separation of matrilines and habitats we present here suggests that habitat specialisations have been in place for many more generations than, for instance, the four generations of spongers which have been observed in ESB so far.

The segregation of mtDNA haplotypes by habitat appears to be driven by vertically transmitted foraging specialisations (and/or other behaviours leading to habitat specialisation). The absence of fine-scale genetic structure based on biparentally inherited markers shows that the correlation of maternally inherited mtDNA haplotype and water

depth cannot be explained solely by geographic separation. Of course, it was possible that there is undetected autosomal structure, but it is most likely that this would be strong enough to secondarily cause the extremely sharp mtDNA patterning that we observed. That any autosomal structuring within our study area must be only weak is supported by two points. Firstly, our use of Locprior ensures detection of relatively week structure [37]. Secondly, the relatively weak autosomal genetic differentiation between ESB and WSB was documented using a much smaller number of markers [30] than used in the current study.

Different depth preferences exhibited by dolphins with different mtDNA haplotypes coincide with different habitats. Seagrass meadows are characteristic of shallow water, and conical sponges only grow in water deeper than 10 m in WSB [23]. Shallow and deep habitats intergrade and are not divided by a barrier or distance that could prevent dolphins from moving between deep and shallow water. The absence of genetic structure based on biparental genetic markers indicates that there is no mating barrier between deep and shallow habitat and may be explained by the dispersal patterns of Shark Bay dolphins. Both sexes are philopatric, with males expanding their natal range [30, 31]. In the WSB study site, we observed the dolphins foraging, travelling, resting and socialising. Therefore the geographic segregation of dolphins with different mtDNA haplotypes indicates that dolphins stay in their natal habitat for all those activities (i.e. we do not know about mating). Male bottlenose dolphins in Shark Bay cooperate with one another in pairs and trios to consort females [42]. It appears that allied males can direct a female outside her regular home range. Some sightings of females with haplotype H in deep water or haplotype E in shallow water might be explained by the coercion of males. It is possible that these groupings involved consorting of females by males, however, we did not confirm the consortships by the standards of ESB [42]. In ESB, males have been observed consorting females never seen

266 in the study site before and well-studied females altered their depth-use during consortships
267 [43].

268 Although our study site is not likely to encompass the entire home ranges of some
269 individuals [44] included in this study, it is about five times the size of an average adult ESB
270 dolphin home range [31]. Accordingly, we expect our identification of each individual's
271 habitat usage to be suitably representative. In addition, the number of resightings per
272 individual (up to 33) suggests that the study site covers a great portion of the home ranges
273 of at least some animals.

274 Our individual-based simulations emphasise that social transmission of habitat-dependent
275 specialisations can lead to fine-scale genetic structure (figure 3, first and second column);
276 whereas this fine-scale structure is unlikely to be seen if there is no social transmission
277 (figure 3, fourth column). Social transmission of foraging strategies in WSB appears likely,
278 given the mtDNA haplotype sharing among WSB spongers, as occurs in ESB [24]. Our finding
279 that spongers in WSB are not more closely related than expected by chance provides further
280 evidence that sponging is transmitted socially, rather than genetically, and in a vertical
281 fashion. Furthermore, our simulations indicate that two specialisations are necessary, one
282 for the deep and one for the shallow habitat, in order to obtain the observed segregation of
283 two mtDNA haplotypes by habitat. It is conceivable that traits other than sponging are
284 vertically socially transmitted, such that matrilines H and F also exhibit habitat specialisation.
285 Without any habitat specialisation, no mtDNA haplotype segregation is observed (figure 3,
286 fourth column).

287 Although all spongers sampled in WSB belong to one matriline, it is a different matriline
288 from that of spongers in ESB [24]. The presence of different sponging matrilines in each gulf

289 can be explained most parsimoniously by the occurrence of at least two independent
290 innovations, one in each gulf. Alternatively, there could have been horizontal transmission
291 between matrilines. However, this would have to be extremely rare to fit the patterns that
292 we observe.

293 What we have inferred for sponging may be just one example of a more widespread
294 phenomenon of interactions between culture and geographic structure of genetic variation.
295 Genetic differentiation on relatively small scales has been reported for many bottlenose
296 dolphin populations (both *T. aduncus* or *T. truncatus*) in all oceans. This structuring was
297 attributed largely to habitat specialisation and was found based on maternal and
298 biparentally inherited markers [45-49]. However, most of these studies (except [45]) gave no
299 indication of what the specialisations might be, or how they could have driven the genetic
300 structure. Furthermore, the geographic scales at which genetic differentiation have been
301 documented (tens to hundreds of km) in previous studies are much greater than those
302 reported here: deep and shallow habitats in WSB are separated by just tens of meters. The
303 largest delphinid, the killer whale, may present a similar case. Sympatric ecotypes were
304 shown to differ genetically and in their foraging behaviour [16, 50]. The genetic
305 differentiation between ecotypes based on microsatellites suggests that this separation may
306 be more stringent and/or has been in place for longer than in WSB.

307 A correlation between habitat and genetic structure has also been found in tool-using New
308 Caledonian crows (*Corvus moneduloides*) [51]. Rutz *et al*. [51] found biparental and maternal
309 (e.g. mtDNA haplotypes) genetic structure among three habitats (dry forest, farmland and
310 beachside habitat, < 10 km apart), in which different tool use has been observed. Restricted
311 dispersal may lead to localised occurrence of particular tool use [51]. In female mountain

312 gorillas (*Gorilla beringei beringei*) and western gorillas (*G. gorilla diehli*), Guschanski *et al.*
313 [52] reported a correlation between microsatellite-based genetic and geographic structure
314 (i.e. altitude). This correlation did not hold for males. In gorillas, both sexes disperse, but
315 females usually join a neighbouring group. Hence, female dispersal distance is limited and
316 often occurs within habitat types. The authors concluded that dispersal usually results in
317 females staying within the habitat into which they were born, probably due to food
318 preferences [52]. Unfortunately, data on maternally inherited markers was not presented.
319 The correlation between habitat and mitochondrial genetic structure in bottlenose dolphins
320 reported here holds for both adult females and males.

321 If vertical social transmission influences the fine-scale genetic structure of a population (e.g.
322 within WSB), it may have consequences for the genetic structure at larger scales (e.g.
323 between the two gulfs of Shark Bay). Since WSB matrilines seem to stay in their natal
324 habitats, it is likely that they have behaviourally adapted to those habitats. If male and
325 female dolphins in Shark Bay are philopatric because of learnt foraging strategies, genetic
326 differentiation would occur – as observed - over small geographic distances. Limited
327 dispersal for both sexes could potentially cause inbreeding. Indeed, elevated levels of
328 inbreeding were measured in ESB, but the costs may not be high enough to outweigh
329 benefits of philopatry [53]. Philopatry bears benefits of habitat familiarity and the potential
330 for kin cooperation [54]. This study highlights that cultural forces can shape genetic
331 population structure outside humans and on a small geographic scale.

332

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510

Table 1: Depth preference of WSB dolphins. Nested ANOVA comparing depth spectra of dolphins with different mtDNA haplotypes. Dolphin ID was used as a random factor nested within haplotypes.

		type III sum of squares	**df**	**mean square**	**F**	**sig.**
Intercept	hypothesis	19563.33	1	19563.33	561.81	< 0.001
	error	3744.74	107.54	34.822		
Haplotype	hypothesis	1320.41	2	660.21	18.31	< 0.001
	error	3824.89	106.09	36.05		
ID(haplotype)	hypothesis	6815.46	87	78.34	13.34	< 0.001
	error	3912.11	666	5.87		

Table 2: Differences in depth preference for dolphins with different haplotypes (WSB). Tukey HSD *Post Hoc* Test for nested ANOVA.

hap 1	hap 2	depth diff. [m]	std. error	sig.	95 % CI depth [m]	
					lower	upper
E	H	5.7*	0.19	< 0.001	5.2	6.1
E	F	1.5*	0.28	< 0.001	0.9	2.2
F	H	4.1*	0.28	< 0.001	3.5	4.8

hap: Haplotype, depth diff.: Mean depth difference, * indicates significance

520 **Figure legends**

521 **Figure 1:** Segregation of dolphin haplotypes by habitats in WSB. Survey locations of dolphins
522 with known mtDNA haplotypes are indicated. Survey colours represent haplotypes of
523 dolphins. Each sighting of a sampled dolphin was plotted, thus individuals can appear
524 multiple times. The sightings include all types of behaviour, including foraging, travelling,
525 resting, socialising and unknown. White areas represent shallow (< 10 m) and grey areas
526 represent deep (> 10 m) water. Insert illustrates the study area within Shark Bay; ESB
527 indicates the location of the eastern gulf of Shark Bay.

528

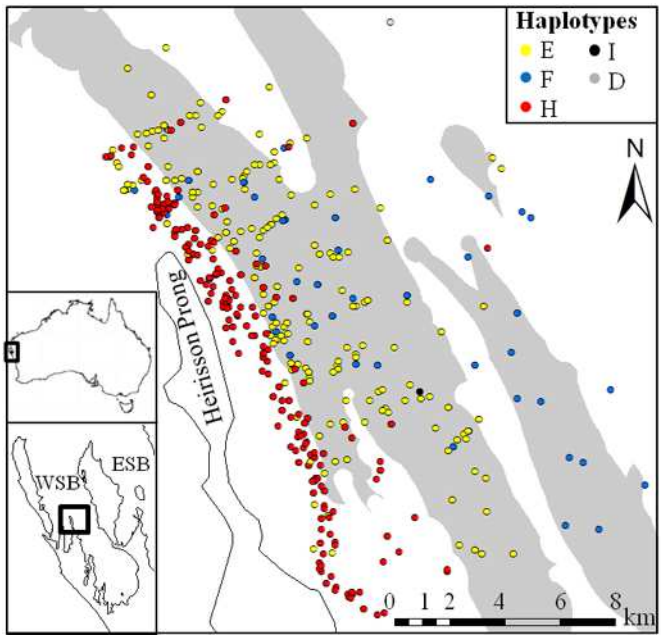
529 **Figure 2:** Depth preference of bottlenose dolphins with the three common haplotypes: H, F
530 and E (sponger haplotype). Boxes contain 50% of data points. Medians are indicated by black
531 horizontal lines within boxes. Whiskers delimit the lower and upper quartiles respectively.
532 Circles and asterisks represent outliers that are more than 1.5 and 3 times the box length
533 away from either end of the box, respectively.

534

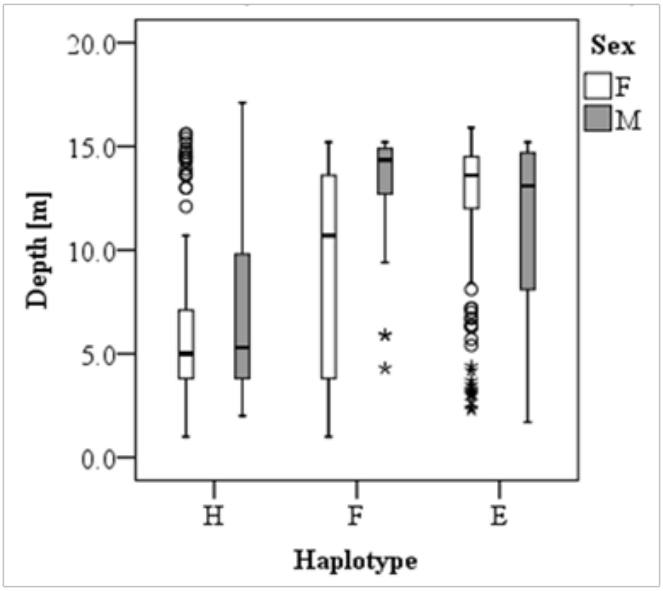
535 **Figure 3:** MtDNA haplotype segregation by habitat in an individual-based model. Three
536 mtDNA haplotypes (Hap1, 2 and 3) and two habitat specialisations (sponging and strategy2)
537 were present. All spongers had Hap1 and all strategy2 individuals had Hap2. Top row:
538 number of different females per strategy (No IDs/strategy). Bottom row: proportion of
539 individuals with a particular mtDNA haplotype in deep water relative to all individuals with
540 this particular mtDNA haplotype. Proportions were calculated for every haplotype
541 separately. Error bars represent one standard error. Dashed lines indicate the observed

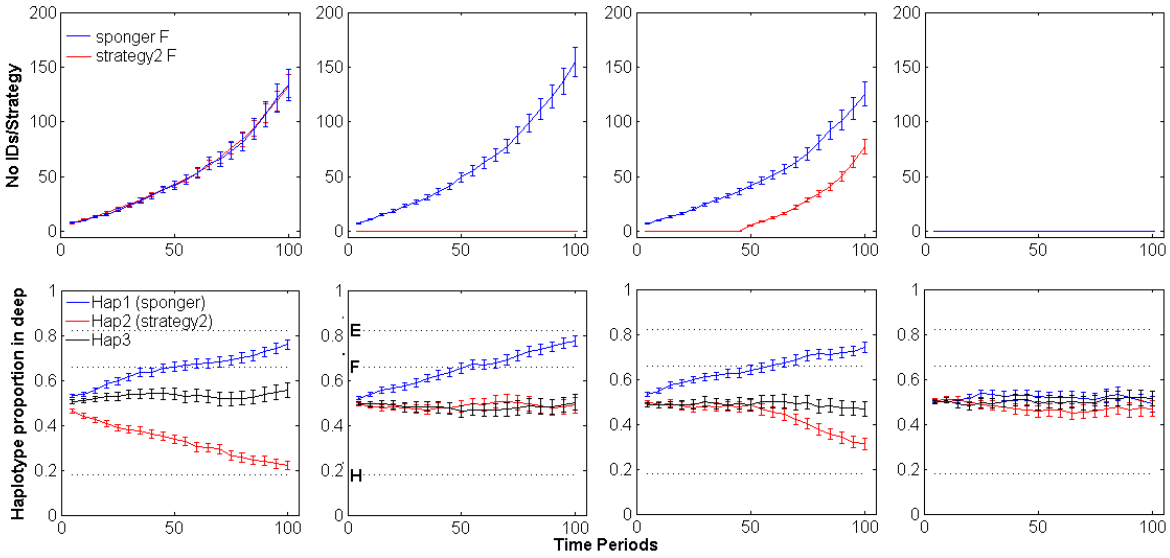
haplotype proportion in deep water for the three mtDNA haplotypes E, F and H in WSB. Fitness benefits for specialists are shown below graphs. Because random cultural drift [55] is a strong force counteracting the establishment of new innovation we indicated the likelihood (%) of at least one specialist/strategy to persist for 100 time periods; this is shown below the fitness benefits. Learning fidelities equalled 1 for daughters born to specialists for the simulations shown here. Simulation results with various other learning fidelities and fitness benefits are shown in figure S3. In the first column, individuals of both strategies had the same fitness benefits. In the second column, only one strategy (sponging) was present, in the third column, strategy2 was innovated 50 time periods after sponging and had a higher fitness, and in the fourth column, there were no specialisations present.

553


Haplotypes
E
I
F
D
H
N
Heirisson Prong
WSB
ESB
0 1 2 4 6 8 km

554


Sex
F
M
Depth [m]
20.0
15.0
10.0
5.0
0.0
H
F
E
Haplotype



Fitness
sponger: 1.05
strategy2: 1.05
13.1%

Fitness
sponger: 1.05
strategy2: n/a
38.0%

Fitness
sponger: 1.05
strategy2: 1.1
18.1%

Fitness
sponger: n/a
strategy2: n/a
100%

555